HOMOLOGIES OF THE WING VEINS OF THE MEMBRACIDAE.[1]

W. D. Funkhouser.

INTRODUCTION.

Since in problems of phylogeny and taxonomy of insects the homologies of the wing-veins are being taken more and more into consideration, it is evident that the available data on this subject should be as complete as possible.

In the work which has been done along this line, certain families of the Homoptera have received but little attention and of these the Membracidæ appear to have been entirely neglected. For this reason, and because of a large personal interest in this group of bizarre insects, this study has been undertaken, hoping that it might be possible to add in some measure to the knowledge of hemipterous wings.

The work was begun two years ago at the suggestion and under the direction of Dr. MacGillivray, then of Cornell University, and has been completed under the supervision of Dr. Bradley, of the Entomological Department of Cornell, to both of whom I am greatly indebted for their most helpful criticisms and suggestions and for access to the specimens in the Cornell collection for examination and comparison.

METHOD.

Of the various methods of approaching the subject of wing-vein homologies, the Comstock-Needham theory[2] that the study should be based on the ontogenetic consideration of the tracheæ which precede the veins has been so fully established and is so applicable to the membracid wing that any other method of procedure in the examination of this highly specialized and complex homopterous type would appear to be the merest guess-work. It has been a source of the greatest satisfaction in the application of this theory to find that the nymphal tracheation has proven in most cases an open index to the adult venation, while the variation and peculiarities of many veins can be traced directly to the behavior of the tracheæ which preceded them.

---

1. Contribution from the Entomological Laboratory of Cornell University.
2. The Wings of Insects, Am. Nat. XXXII and XXXIII, 1898, 1899.

According to this theory the knowledge of homologies is dependent upon two methods of investigation. First, the ontogeny of the wing of the individual, as based on the study of the tracheation of nymphal wings traced through their successive stages of development, and second, the study of the wings of adults worked out by careful comparison with forms representing known types of venation. Of these two methods, the former has been the one used almost entirely and the second has been resorted to only for those forms for which the nymphs were not available. Since, however, the venation of the Membracidæ is comparatively uniform, the determination of homologies, after the tracheation of the nymphs of the more prominent types has been ascertained, has proven a relatively simple matter.

TECHNIQUE.

The laboratory methods followed have been in the main those outlined in the "Wings of Insects"[3] with such modifications as have been suggested by the condition and shape of the individual wings under consideration.

The wings were dissected from nymphs of various stages of development, but it was found that in most cases the last two instars showed best the features desired. In these two instars the nymphal wings may be pulled out of the wing-pads and are thus more easily studied. In the earlier stages, and in all of the stages of some of the smaller species, e. g. *Vanduzea arquata* or *Micrutalis calva*, it is difficult to remove the wing from the pad without disturbing the position of the tracheæ, and in these cases it is necessary to photograph through the pad membrane. The wings were carefully dissected out, together with a portion of the thorax to show the basal tracheation, and mounted at once. It was found that fresh material gave much better results than that which had been preserved, even for a short time, in formol or alcohol. In many cases, several hundred dissections were made for the verification of some particular point in question. The greatest difficulty was to preserve the tracheæ for a sufficient length of time to secure photomicrographs or careful drawings, since the tracheæ fill in a very short time with the mounting media and are then invisible. Moreover,

3. American Naturalist, Vol. XXXII, p. 45.

in the membracid wing, there is a sharp bend at the point at which the tracheæ enter the body and it is difficult to secure a mount in which the base and tip of the wing are in focus at the same time.

Various mounting media were tried, but for the wings of this family glycerin jelly was uniformly the most satisfactory. A drop of jelly was placed on the slide, the wing laid in the jelly, another drop placed on the cover-slip and the latter placed at once over the specimen. The mount was then quickly cooled by placing a drop of ether on the cover-slip and fanning it to insure rapid evaporation. Some of the mounts made in this way have remained in good condition for over a year and bid fair to last for a much longer period.

Photomicrographs were then made of the specimen, using whatever combination of objective and bellows were necessary to bring out the desired details and to make the image fill a 5x7 plate. Since many of the nymphal wings are less than two millimeters in length, the magnification is necessarily great, but negatives can usually be secured sufficiently sharp to show the points in question. Artificial light, secured by means of a Nernst lamp and series of condensers, seemed to be more desirable than sunlight for this work, mainly owing to the fact that it was possible to secure a chart of uniform exposures for the different magnifications.

In cases where photomicrographs were not considered necessary, careful camera lucida drawings were made, verified by repeated comparisons. For the adult wings, the permanent mounts (Canada balsam) of the wings themselves were used, copied by projection drawings when figures were desired.

Velox and solio prints from all negatives were made for permanent records in this study. The figures of nymphal wings shown in this paper, however, are blueprints inked in with india ink and afterwards bleached.[4] The figures of adult wings are pen drawings made from the permanent mounts with the aid of the camera lucida or projection apparatus.

4. In a saturated solution of Potassium Oxalate.

MATERIAL

Nymphs

About twenty species of the Membracidæ, representing eight genera of fairly wide distribution as regards relationship are common to the local fauna of Ithaca, New York, the nymphs of most of which are easily obtainable. These have been used for the determination of the nymphal tracheation. The choice of the various species studied has depended largely upon the characters of the adult wings. In cases of closely related forms where the venation was practically identical and no special problems were involved, the nymphs of a representative species only have been thoroughly worked not, except for the solution of certain questionable points. Some nymphs, also, owing to the form of the wing yield much better preparations than others, and these have been more elaborately figured where general characteristics only were being considered. Some have been discarded because of lack of positive identification and others because of the fact that they were less abundant and illustrated no features not found in forms more easily procured. The bulk of the work has been done from nymphs of the following genera: *Ceresa* (*bubalus*, *diceros* and *constans*), *Thelia* (*bimaculata*), *Telemona* (*ampelopsidis*), *Vanduzea* (*arquata*), *Campylenchia* (*curvata*) and *Enchenopa* (*binotata*). Altogether several thousand dissections have been made and each point in tracheation has been as carefully verified as possible. No attempt has been made to breed the insects since extensive field notes on the habitat, hosts, life-history and general biology of the local forms has made it possible to procure the nymphs at various stages without particular difficulty.

Adults

Besides the forms represented in the local fauna, the wings of all other species procurable have been studied with the view of obtaining a large number of types of venation. The writer is greatly indebted to the Entomological Department of Cornell for the privilege of examining the wings of all the species in the excellent collection of the University, which includes many forms that could not otherwise have been obtained. Thanks also are due to Dr. J. C. Bradley and to Mr. C. R. Plunket for the use of specimens from their collections.

Six subfamilies are recognized in the Membracidæ by the systematists in Hemiptera[5] and representative genera from all sub-families reported from the United States[6] have been examined. Wings from the following genera are figured in this paper as representative:

Smiliida
- *Cerasini*
  - Ceresa
  - Stictocephala
  - Acutalis
  - Micrutalis
- *Telamonini*
  - Carynota
  - Thelia
  - Glossonotus
  - Telemona
  - Telemonanthe
  - Archasia
  - Heliria
- *Smiliini*
  - Smilia
  - Cyrtolobus
    - Cyrtolobus
    - Atymna
    - Xantholobus
  - Ophiderma
- *Polyglyptini*
  - Vanduzea
  - Entylia
  - Publilia

Darnida
  - Stictopelta

Hoplophorida
  - Platycotes

Membracida
  - Campylenchia
  - Enchenopa
  - Tylopelta
  - Philya

Centrodita
  - Centruchoides
  - Platycentrus

(The above classification is based on that of E. P. VanDuzee in his "Studies in North American Membracidae," Bulletin of Buffalo Society Natural Science, 1908, Vol. IX.)

---

5. Cf. Stal, Hemiptera Africana IV, pp. 82–83.
Goding, Bibliographical and Synonymical Catalogue of the Described Membracidae of North America. Bull. Ill. State Lab. Nat. Hist., Vol. III, Art. XIV, p. 302.
VanDuzee, Bull. Buffalo Soc. Nat. Sci. 1908, Vol. IX, p. 31.

6. According to VanDuzee (Studies in North American Membracidae, p. 31) the Tragopida are not represented in this country. Moreover in this sub-family the fore wing at least is coriaceous and opaque externally, and would probably be of little value in the study of venation.

In addition to the species actually examined, careful comparison has been made with as many figured wings of the Membracidæ as could be located[7] and it has been a satisfaction to note that in practically all cases there is a constant and easily worked out agreement with the homologies as herein suggested.

Since the Membracidæ is principally an American family, only a few genera being found on the continent of Europe[8], but two species in Britain[9] and very few reported from other parts of the world, there seems no reason to believe that our local forms in New York should not be typical of the family. Moreover, the venation is quite uniform throughout the family and it appears reasonable to suppose that the homologies as here worked out for the representative genera figured will be readily applicable to the entire Membracidæ.

NOMENCLATURE

Many of the specific, generic and sub-family distinctions in the Membracidæ are dependent upon the venation, and most tables and keys to the family follow the nomenclature of Fowler, Goding and others in which the characters of the cells are used as a basis of classification. Little attention has been paid to the veins except as to their number at the base of the wing or as forming the "petiole" of a cell.

The cells are called "areoles" or "areas" and are described as "marginal", "discoidal", "apical", "anterior", etc., and their bases as "petiolate", "truncate", etc., but little attempt has been made to identify the veins which limit these cells. Fowler in his discussion of the Ceresini in the Biologia[10] describes the "costal", "radial" and "ulnar" veins, and this nomenclature has been used to some extent by other writers.

The fore wing is commonly spoken of as the tegmina and its venation often designated as the elytral venation. The hind wing is referred to as the under wing or the second wing. The corium is often discussed separately, as is also the clavus

---

7. In the plates of Canon Fowler in the Biologia Centrali Americana particularly, the figures, while representing forms foreign to our fauna, are evidently very accurately reproduced and agree to a remarkable extent with our North American species, so far as venation is concerned.

8. Canon Fowler. Bio. Cent. Amer., Insecta: Rhynchota, Homoptera. Part II, p. 2.

9. Cambridge Natural History, Insects Part II, p. 577.

10. Biologia Centrali Americana, Insecta: Rhynchota, Homoptera. Part II, p. 87.

and the membranous margin, and altogether a rather complex and imposing accumulation of terms has been built up, not at all contradictory, but somewhat confusing.

It would be entirely unnecessary and out of place at this point to enter into the controversy regarding the systems of nomenclature of wing-veins and their respective merits, a subject which has been thoroughly and repeatedly reviewed[11]. The nomenclature used in this study is entirely that of the Comstock-Needham system, and therefore the veins and cells here described conform to those represented in other work done according to this system. The names "costa", "subcosta" "radius", "media", "cubitus" and "anal" will be used throughout. Thus the "terminal areole" of VanDuzee, the "third apical area" of Fowler and the "celule terminale" of Fairmaire becomes cell R^5 as dependent on the homology of the vein R^5, and will be so designated in this discussion, and this same system will hold for all other veins and cells discussed.

THE MEMBRACID WING

The Membracidæ is one of those families of the Homoptera in the wings of which the corium and clavus are usually membranous, the veins in most forms are distinct, there is practically no thickening at the base of the wing, and both pairs of wings are well developed (Fig. 1). These features are better shown in the membracid wings than in those of any of the other Hemiptera with the possible exception of the Cicadidæ. The wings are well adapted for flying and the insects fly well for short distances with a whirring noise.

The fore wings are large, expanded and distinctly veined. They are usually membranous throughout, but occasionally show coriaceous patches and basal punctures, especially along the anterior margin. The clavus[12] is distinct, the claval suture

---

11. The historical discussion of the nomenclature of wing-veins is taken up in detail by Dr. A. D. MacGillivray in the "Wings of Tenthredinoidea," Proc. U. S. Museum, 1906, Vol. XXIX, pp. 570–574.

Miss Edith M. Patch reviews the terminology of homopterous wing venation in "Homologies of the Wing-Veins of the Aphididae, Psyllidae, Aleurodidae and Coccidae," Annals Entomological Society of America, 1909, Vol. II, pp. 124–126.

Cf. also C. W. Woodworth, The Wings of Insects. University of California Publications, Agricultural Experiment Station Technical Bulletin, Entomology, Vol. I, p. 142.

12. In the hemipterous wing the basal portion consists of two pieces. The term "clavus" is here applied to the narrow posterior piece which is next to the scutellum when the wing is closed. This is figured in Comstock's "Manual for the Study of Insects," p. 124.

occurring along the first anal vein. There are few cross-veins but those present are remarkably constant. The wing may or may not be covered by the pronotum, but in no case is it to be considered in the sense of an elytron.

The hind wing is not nearly so dissimilar to the fore wing as is the case in most insects. C. W. Woodworth in the "Wings of Insects"[13] remarks that "the hind wings of most of the families of Homoptera have more nearly kept pace with the front wings in their specialization, than have those of the Heteroptera". This is certainly true of the Membracidæ. There are fewer veins and cells in the hind wing than in the fore but their homologies are evident.

Both wings are characterized by the strongly scalloped margin of the veined surface and the comparatively narrow terminal membrane.

Like most of the other Hemiptera, the wings of the Membracidæ are specialized by reduction, but the reduction has not been carried so far as in most of the other families of this order. This reduction has been carried on in two ways, viz.: by atrophy and by coalescence. Reduction by atrophy is shown by costa in both wings. Coalescence, in turn, has been accomplished by two methods—by coalescence from the base towards the margin, as illustrated by cubitus, and by the anastomosis of veins in the center of the wing followed by their subsequent divergence, as shown in the case of radius four-plus-five plus media one-plus-two. No cases have been noted of coalescence from the margin proximad.

However, no hint of the particular veins in which this specialization occurs is given by the venation of the adult wing, and it is only by following the nymphal structure, trachea by trachea, and branch by branch, that the actual solution can be reached with any degree of accuracy.

NYMPHAL TRACHEATION

A study of the most general characteristics of the nymphal tracheation may well be made before proceeding to the consideration of the minutia. In the fore wing (Fig. 2), it will be noted that there are five main tracheæ. Beginning at the anterior margin, the first is unbranched and extends almost to the tip of the wing. The second appears two-branched and the posterior branch anastomoses for some distance with the ante-

13. Univ. of Cal. Publ., Ag. Ex. Sta. Tech. Bull. Ent., Vol. I, No. 1, p. 124.

rior branch of the following trachea. There is also a suggestion of splitting near the base of the anterior branch. The third is two-branched with the anastomosis as noted. The fourth is two-branched, the tracheæ separating very close to the base of the wing. The last is also two-branched with the branches coalescing at their extremities.

The relationship of these treacheæ with the corresponding wing veins is evident. Their identification as regards the homologies of wing veins in general is not so simple a matter. For this reason the veins as dependent on these tracheæ will be discussed in order, beginning at the costal margin.

FORE WING

Costa

Costa never appears as a separate vein in the adult wing. It was some time in the course of this study before sufficient data was obtained to determine exactly what had become of this vein, since most of the preparations failed to show a corresponding trachea in the nymphal wing. Finally however, an examination of younger stages of various species furnished the solution. In Thelia bimaculata (Fig. 3) it was found that costa was represented in the nymphal tracheation but never entered the wing for a sufficient distance to have a place in the adult structure. In most individuals the atrophy was greater than that shown in the figure. In *Telemona ampelopsidis* (Fig. 4) the treachea is twisted around the subcosta and no doubt coalesces with it in the vein which afterwards encloses them. In *Ceresa borealis* (Fig. 5) the trachea extends farther into the wing but is not so well developed and probably has no effect on the venation. In *Vanduzea arquata* (Fig. 6) much the same appearance is shown except that the trachea is stronger and lies nearer the margin of the wing.

To sum up then, the trachea which usually precedes the costal vein *is* represented in the nymphal structure but the vein itself is not found in the adult wing. In such genera as *Thelia*, *Acutalis* and *Glossonotus*[14] in which a slight membrane is found cephalad of subcosta but no thickened ridge is present, the vein is probably atrophied[15].

14. All forms mentioned are figured either through the text or at the end of the discussion. The figures of adult wings are drawn to show the coalescence of tracheae to form a single vein when such has been the case.

15. This is no unusual condition with costa. Comstock and Needham say (Wings of Insects, p. 858). "Its (costa's) trachea is often atrophied, probably owing to the disadvantageous position of its base in relation to air supply, as we have hitherto indicated."

In *Ceresa*, *Micrutalis*, *Telemona*, etc., in which subcosta forms the cephalic margin, the tracheæ for costa and subcosta have coalesced. In *Heliria*, *Vanduzea* and *Enchenopa* the trachea has had an influence on the costal margin to form a thickening near the base of the wing.

Subcosta

Subcosta is constant in character throughout the family. It is strong, straight and unbranched and extends the full length of the wing (Fig. 2). It is the anterior vein of the wing, owing to the atrophy of costa, and as such often forms the cephalic margin. In the sub-families Hoplophorida and Membracida[16] the vein is usually contiguous to the anterior margin for its basal half, and then drops down, leaving a terminal membrane anterior to its distal half. Sometimes this membrane occurs down the entire cephalic margin. No splitting occurs at the end of the vein. It sometimes anastomoses with parts of radius as will be shown in the discussion of that vein, but this is due to the peculiarities of radius and to no irregularities on the part of subcosta. Its base occasionally shows a fullness or slack which later straightens out in the vein formation (Fig. 7). Altogether, subcosta is always permanent, straight, clean-cut and independent, both in its tracheation and in its final structure.

Radius

The behavior of radius offered one of the most difficult problems of the membracid wing. Instead of the typical five-branched condition (Fig. 8) we have in the venation of this family (Fig. 2) what is seemingly a two-branched condition, with what appears to be a cross-vein connecting the cephalic branch with subcosta. This, in itself, would offer but little difficulty, since if the reduction of the five-branched type were carried far enough by coalescence outward, it would give a two-branched result. The natural method of reduction of radius is by the coalescence of the branches of each half of the radial sector, leaving the sector two-branched and the vein as a whole three-branched. If the same method of reduction be carried further, R_1 and the sector only are left, giving a two-branched condition of the whole vein.

16. See figures of Platycotes, Phylia, Campylenchia and Enchenopa. Nos. 51, 52 and 53.

But in the Membracidæ several points not compatable with this natural method of reduction presented difficulties. In the first place, both branches showed constant and unmistakable signs of further subdivision at their tips, which would not be likely to be true of the cephalic branch if it were R_1. Moreover, the vein between the cephalic branch and subcosta was often seen to be preceded by a trachea. Again and again in mounts of different species this area contained a trachea which was evidently a branch from the cephalic branch of radius. If this were true, this most anterior branch should be R_1. But R_1 normally leaves the main stem proximad of the division of the radial sector, while this branch seemingly pulls off from one half of the sector itself, and this demanded an explanation which was not immediately forthcoming.

The solution was first found in the wings of *Vanduzea arquata* and later this peculiar condition (Fig. 9) was verified in other genera. The trachea representing R_1, as will be seen from the figure, is weak and apparently greatly reduced. It leaves the main stem in the normal postion, but runs in close juxtaposition to the radial sector beyond the point at which the latter branches. Here it turns cephalad and runs across to subcosta where it again turns outward and closely parallels subcosta for some distance in its course toward the tip of the wing. The sharp turns made by the trachea in following this course (Fig. 10) are remarkable, and in the veins which enclose this region of the wing, the bridge from radial sector to subcosta (Fig. 11) gives every appearance of a cross-vein.

While this interesting behavior of R_1 is unusual, and perhaps peculiar to the Membracidæ, it only illustrates another of the vagaries of which radius is capable. In fact, throughout the Hemiptera, radius seems to be most unreliable, and R_1 capable of the most peculiar performances, being, according to Miss Patch[17] "the least stable of the hemipterous wing veins". It has been shown in the Cicadidæ[18] that R_1 has been crowded by subcosta until its trachea coalesces for its entire length with radial sector and its anterior branch. In the Pentatomidæ[19] also, it has been supplanted by subcosta and is entirely

17. Annals of the Entomological Society of America, 1909, Vol. 2, p. 119.
18. Wings of Insects, p. 245.
19. Wings of Insects, p. 250.

atrophied. In the Coreidæ[20] R_1 is wanting. The weakness of the vein has been remarked in the Aphididæ[21] and it is entirely lacking in the Psyllidæ[22] and in the Aleurodidæ[23]. In fact, Comstock and Needham state[24] that the complete absence of the vein R_1 is one of the most characteristic features in the venation of the wings of the Hemiptera.

It is of some phylogenetic interest, then, to note that in the Membracidæ, while the vein is abnormal, it is *not* completely absent, and in this respect the membracid wings may be considered the most generalized of any of the families of Homoptera, at least those of which the homologies of wing-veins have been determined.

Most of the genera of the Membracidæ show the position of R_1 as described. In many it has been impossible to find the trachea, although the vein is present and constant. Since, however, the history of the vein is evidently traceable to the trachea representing R_1, it seems necessary to call this vein R_1 whenever it appears.

In a few genera, namely, *Acutalis*, *Tylopelta*, *Enchenopa*, *Campylenchia*, *Platycentrus*, and *Centruchoides*, the vein comes off in its normal position. In the nymphal wings of *Enchenopa binotata*, for example (Fig. 12), the trachea is found in its natural place. These genera are, of course, still more generalized with regard to this special point, but are not so typical of the family.

The course of the rest of radius is evident from the tracheation. At its base it often anastomoses for some distance with media before these two principal veins separate for their respective courses through the wing. In *Ceresa*, *Stictocephala*, etc., this coalescence must be fairly constant, since it has been made a basis for classification[25]. R_{2+3} usually extends undivided to the tip of the wing. It is generally connected with R_{4+5} by a cross-vein. R_{4+5} is represented as one vein and coalesces with the anterior branch of media (M_{1+2}) for a more or less extended part of its course. The amount of coalescence

20. Wings of Insects, p. 252.
21. Annals of the Entomological Society of America, 1909, Vol. II, p. 111.
22. Annals Ent. Soc. of Amer., 1909, Vol. II, p. 119.
23. Annals Ent. Soc. of Amer., 1909, Vol. II, p. 122.
24. Wings of Insects, p. 245.
25. Biologia Centrali Americana, Insecta: Rhynchota, Homoptera, Part II, p. 87.

shown in figure 11 is about the average. In a few species[26] the course is more extended, and in some[27] the veins do not coalesce at all but run some distance apart, connected by one or more cross-veins. Just before reaching the tip of the wing, however, this vein separates from media to make the apical or terminal cell, which is thus cell R_5. The tips of both branches of radial sector show signs of splitting in their tracheal condition. In some cases they actually remain separate and form additional cells in the wing. This is true of the species *Telemonanthe pulchella*, *Cyrtolobus vau* and *Smilia camelus* (see figures Nos. 39, 43 and 42). In the first, R_2 and R_3 are separate. In the second, a very small cell R_4 appears, showing that R_4 and R_5 have not entirely coalesced.

In this species also, a peculiar condition of R_3 is shown, the end of the vein still persisting at the margin of the wing, while its base has disappeared. In *Smilia camelus*, R_3 has not entirely coalesced with R_2, and extends into the cell R_{2+3} where it is perhaps atrophying back toward its base. This means that in these forms the reduction has not proceeded so far as it has in the majority of the species.

Summing up, then, radius is typically three-branched in the Membracidæ. R_1 extends from R_{2+3} to subcosta. R_{2+3} and R_{4+5} usually extend as undivided branches, with the exceptions noted, to the tip of the wing, R_{4+5} ordinarily anastomosing for a variable part of its length with M_{1+2}.

Media

The course of media (Fig. 13) is quite constant. Starting from the base of the wing in close proximity if not in actual contact with radius, it follows a relatively straight course for about two-thirds of the wing length. It represents the most posterior vein of the costa-subcosta-radius-media group, and its origin is intimately connected with the stem of these veins (Fig. 14). In such forms as *Acutalis*, *Micrutalis*, *Thelia*, and *Carynota* of the Smiliida, this close connection is not shown in the adult wing. In others, as *Ceresa* and *Stictocephala*, the relationship is striking, as has been referred to in the consideration of radius.

26. e. g., *Cyrtolobus vau* and *Atyma castaneae*.
27. *Platycotis sagittata*, *Enchenopa binotata*, *Campylenchia curvata*, *Centruchoides perdita*, and *Platycentrus acuticornis*.

In the distal third of the wing, media branches into M_{1+2} and M_{3+4}, the upper branch usually but not always uniting with R_{4+5}. This is, in most cases, the end of its branching, since the reduction by coalescence outward has obliterated the individual veins M_1, M_2, M_3 and M_4. In a few cases these veins persist to the point of forming an extra marginal cell. This is true of *Archasia belfragei* and *Ophiderma pubescens*, where M_3 and M_4 are separate, and in *Micrutalis dorsalis* where M_1 and M_2 show a very slight space between them. In the latter species this feature, which has been remarked by VanDuzee in a taxonomic sense[28], is not always constant. In *Smilia camelus*, M_4 has behaved much as has R_2 in the same species (see radius) by extending part way into cell M_{3+4} and probably atrophying toward its base. A peculiar condition is shown in *Xantholobus trilineatus* in which M_1 and M_2 have not coalesced, thus leaving a cell M_1. M_3 has coalesced with M_2 near the margin of the wing to form the unusual combination M_{2+3}. M_4 extends part way into cell M_{3+4} as was seen in the case of Smilia.

On the whole, media represents a simple, natural reduction and is one of the most constant veins in the membracid wing.

Cubitus

With the consideration of cubitus comes a perplexing problem in interpretation. There is no doubt as to the tracheation, which is constant throughout the family, but the homologies are not at once evident. From the posterior base of the wing, and separate from the costa-subcosta-radius-media group, come two distinct main stems (Figs. 5 and 15). These must represent cubitus and the anals. The upper stem is typically two-branched which is characteristic of cubitus; the lower is three-branched and seems naturally to be First, Second and Third Anal respectively (Fig. 16). Certain features, however, make this interpretation unacceptable. The first and most important of these is the fact that the point of branching of the anterior trachea occurs so far back in the nymphal wing that it would not appear, and does not appear, in the adult venation. This is entirely inconsistant with the reduction which has taken place in all of the other veins of the same wing, and it is inconceivable that while coalescence outward has been taking place

28. Studies in North American Membracidae, p. 52.

in all the rest of the wing, cubitus has been dividing in the opposite direction. Moreover, the end of the cephalic branch shows, as did radius and media, unmistakable evidence of a doubly tracheated condition (Fig. 17). At first this was considered as a mere splitting of the end of the trachea and was disregarded. It appeared so constantly, however, and at times extended so far back into the wing, that it refused to be ignored. Again, it has been shown in other families of the Homoptera, that the first and second anal veins may be widely separated[29], the first anal arising from the cubital stem. In view of these facts then, it appears that the most anterior branch of the upper vein represents both Cu_1 and Cu_2. That these veins have coalesced outward in the regular manner, forming one vein only in the adult wing, although the two tracheæ are distinguishable in the nymphal condition. This interpretation makes the position of the anal fold in the membracid wing agree with the position which it assumes in the other Hemiptera, namely, along the first anal vein. If the next vein (First Anal) were considered as Cu_2 it would make the Membracidæ peculiar in this respect, and not in keeping with the conditions in the closely related families.

The trachea runs parallel with media for about half the length of the wing and then makes an abrupt turn downward, running to the posterior margin. At this point it divides, the two branches however never separating but turning together outward again toward the tip. The vein which encloses them follows this course without deviation. Just after the vein makes the sharp turn caudad, a strong cross-vein connects it with M_{3+4}. This cross-vein (medio-cubital), as will be shown later, may be of varying length but is constant and very characteristic of the family. It well represents one of the points which brings out the importance of the study of tracheation. In the adult wing (Fig. 1) it might well be taken for a branch of cubitus, but the nymphal wing (Fig. 18) clearly shows that it is not preceded by a trachea. A careful search has been made through hundreds of mounts to establish this point, and no case has yet been found where this condition was not true. On the theory that the principal veins are preceded by trachea while the cross-veins are not, this would prove that the vein in question could not be a part of cubitus.

29. Wings of Insects, p. 249.

The Anal Veins

If the interpretation of the preceding structures has been correct, the remaining veins of the wing must represent the anals. As a matter of fact, this works out very simply and leaves little doubt regarding the homologies of the anal region. It is true that the third anal often shows a forking in the nymphal tracheation (Figs. 5 and 16), but this is of no particular consequence since in a very large number of wings, of which that of the cockroach may serve as an example[30], the anal region has become filled with many veins branching from or posterior to the third anal. In fact, this condition (Fig. 19) homologizes perfectly with the tracheation of this vein in the Cicadidæ[31] which family is as close to the Membracidæ as any whose venation has been determined, and in which, as in the Membracidæ, the specialization has been by reduction. A more significant fact is that this condition is by no means a constant one and should not be considered as typical of the family. In the large majority of cases the anal tracheation is best represented by that shown in Figure 2.

According to this determination, then, the first anal vein arises from the base of cubitus with which stem it has been brought from the main trunk. If this is true, the first anal is very intimately connected with the cubital vein — so intimate, in fact, that it seems almost a misnomer to call it an anal with reference to the Membracidæ — but that it is an anal is shown by the fact that it homologizes with the first anal in the wings of other insects. It represents the claval suture in the fore wing and is in many forms very indistinct in appearance, and the wing is weak along the line which it follows. It is straight and unbranched throughout its course and is connected with no cross-veins. At its tip it unites with cubitus, and the two coalesce to form the marginal limiting vein of the cell M_4. This limiting vein, it must be remarked, is here preceded by three tracheæ, viz. Cu_1, Cu_2 and 1st anal.

Second anal and third anal enter the wing together by a different stem, posterior to that of the cubitus-first anal. They separate at once, forming a large and clearly defined cell, only to coalesce again after about one-third of their course has been

30. Wings of Insects, p. 773.
31. Wings of Insects, p. 249.

traversed (Fig. 20). In this condition they join first anal just before that vein unites with cubitus at its distal end.

This represents the normal proceduré. It is not strange to find, however, in a reduced wing, that this region is subject to more variation than that of any of the other veins. In some species, for example, third anal never appears in the adult wing and the cell 2nd A is absent. This has been brought about either by the atrophy of third anal or by its coalescence for an entire instead of a partial length with second anal, the latter explanation being perhaps the more reasonable. Since this condition is found principally in the wings of the smaller species such as *Micrutalis calva*, *Stictocephala lutea*, and *Cyrtolobus vau* (see figures 33, 31, 43) it is probably due to the lack of development of this part of the wing, which causes a crowding of the tracheæ cephalad. In other forms third anal breaks away from second anal after anastomosing for some distance, and sends a very short portion out through the membrane to the margin of the wing. This is found mainly in the larger wings, where there is more surface to be supported, being best seen in the fore wings of *Thelia bimaculata*, *Telemona ampelopsidis*, and *Platycotis sagittata*.

Cross-veins

Of the cross-veins which appear in the fore wing, three only are constant and characteristic of the family, the others being peculiar to certain genera and species and of little comparative importance.

The first of these characteristic cross-veins is found connecting R_{2+3} with R_{4+5}, dividing the cell R_3 at about one-third its length from the point of branching of radial sector. It is fairly constant, but it does not appear in the genera Acutalis or Micrutalis in so far as representatives of these genera have been studied. In the figured wing of *Ophiderma pubescens* q. v., this cross-vein is forked, a condition which is of course abnormal.

The second is equally constant but surprisingly variable in position. It appears between media and cubitus, usually in the basal third of the wing, but often shifts from a position close to the base of these veins (cf. *Ceresa diceros*) to one so far toward the tip of the wing that in the case of *Smilia camelus* (see figure) it has actually moved off of cubitus and its posterior end rests on the other cross-vein which connects Cu with M_{3+4}.

Thus it is the most unreliable cross-vein so far as position is concerned, which is found in the wing. In a few species it does not appear. In *Archasia belfragei*, media and cubitus dip toward and touch one another at the point where this vein is typically found. In *Entylia bactriana*, which is an interesting wing in other respects also, media and cubitus anastomose for such a distance as to make this vein unnecessary. The same is true of *Publilia concava*. In certain forms this vein varies within a species. The figures shown of *Thelia bimaculata* and *Carynota mera* show two cross-veins at this point, but this is only occasionally found even in those species.

The third constant cross-vein is that connecting M_{3+4} with Cu. It varies in length from a mere attachment, as in *Entylia bactriana*, to the prominent and important position which it assumes in most of the wings of the family. No membracid wing has been examined in the course of this study which did not show this cross-vein, and as has been suggested in the consideration of cubitus, it has been particularly noted as being an apparent part of that vein.

Other cross-veins are found, but with no regularity and of no especial significance. R_{4+5} occasionally does not unite with M_{1+2} and a cross-vein bridges over (e. g. *Platycotis sagittata*). M_{3+4} sometime moves so far from M_{1+2} that this part of the wing has been strengthened in the same manner and one species at least has added cross-veins to such an extent that the actual condition of the typical form is only conjectural from the material at hand. This species is *Phylia ferruginosa*, the species possessing the most unusual cross-veining of any Membracid studied.

The tracheation of the wing-base

In their basal structure the wings of the Membracidæ refuse to agree exactly in structure with those of closely related families, and if the determination of homologies in this study is correct, they more nearly approach the hypothetical type than do any of the other Hemiptera.

It has been shown in the wing of the Cicada[32] that all the tracheæ in the wing arise from one main trunk[33]. In the closely related family of Membracidæ it would naturally be

32. Wings of Insects, pp. 243–249.
33. Wings of Insects, p. 244, Fig. 14 and the accompanying discussion.

supposed that this important feature would also hold true, but this appears not to be the case. Instead, the tracheæ arise from two main trunks, the most anterior of which gives rise to costa, subcosta, radius and media, while the other furnishes the origin of cubitus and the anals.

The two trunks come from the thorax at different angles, and so far as has been observed, are never united (Fig. 21). This does not prove, to be sure, that the connection never occurs, but it would seem that in the study of a very large number of nymphal wings the connection would sometimes have appeared if it were present. On the contrary, the study of a long series of wings of many genera and species seems to show that in this particular family the original hypothetical type of two main trunks has been preserved and that in this respect at least, the Membracidæ can be said to be the most generalized of the Hemiptera, being more conservative in this particular than even the Cicada.[34]

Marginal Veins

The scalloped appearance given to the venation by the marginal vein inside the membrane, is characteristic. The extremities of the longitudinal veins are connected by strong regular veins which form a smooth edge for the veined portion of the wing (Fig. 1). The origin of this structure is explained by the manner in which the ends of the longitudinal tracheæ branch and overlap when they reach the region under consideration (Fig. 22). Since the reduction of the wing has left at the tip branches of radius two-plus-three, radius four-plus-five, media one-plus-two, media three-plus-four and cubitus one-plus-two which have not entirely coalesced, it is natural that these tracheæ, which have probably in the wing of past times represented separate veins, should remain more or less distinct. This has happened, and the wing tip shows that these tracheæ tend to pull apart and run along the marginal lines (Fig. 23). It seems rather remarkable that any of these tracheæ should ever actually turn backward, but such is the case. The normal method is as follows: subcosta continues along the cephalic margin to the extreme tip of the wing; R_1 unites with subcosta

34. Comstock and Needham state, "The conservative Hemiptera that retain most perfectly the fashions of ancient times so far at least as concerns the venation of the wings, are the cicadas."—Wings of Insects, p. 243.

from the point of its coalescence outward; R_2 turns upward to meet Sc plus R_1; R_3 turns outward and downward and coalesces with the tip of R_4; R_4 turns upward to unite with R_3; R_5 continues outward to touch the end of M_1; M_1 bends upward to R_5; M_2 turns backward to unite with the tip of M_3; M_3 continues forward to meet M_2; M_4 also turns backward to meet the tracheæ of Cu_{1+2} and 1st A which have continued outward, and the tips of the other tracheæ have proceeded distad in their natural position, extending to points which enable them to coalesce with the tracheæ ahead.

In this way a strong marginal vein has been formed along the lines laid down by these tracheæ which is as strong and sometimes stronger than the longitudinal veins themselves, since it contains at various places in its course, the tips of two, three, and sometimes even four tracheæ.

Variation

This study would be incomplete if some mention were not made, in the consideration of the fore wing, of the variations which often occur. The venation which has been outlined has been in the main that of the normal structure. Considerable variation occurs, however, often within a species, and this deserves some mention.

The wing of *Thelia bimaculata* has been chosen as an illustration because this species shows perhaps the greatest range of variation found in any one species. In the diagram shown (Fig. 24) the dotted lines represent the maximum variation, and all stages between the normal and this maximum may be found. It will be noted that R_1 sometimes leaves radius two-plus-three at a point very close to the fork of radial sector. This would represent a less specialized condition than the normal. R_{4+5} and M_{1+2} sometimes approach each other with a wide curve and barely touch, instead of coalescing in the usual manner, and this does away with the sharp bend of M_{1+2}. M_3 and M_4 are occasionally separate, forming an additional cell M_3. As might be supposed from the discussion of the cross-veins, that one between media and cubitus shows the greatest irregularities. It ranges from the most proximal position shown by the dotted lines at the left, to one very close to the point at which media branches, and in some cases even disappears altogether, media and cubitus bending toward and touching each other.

Such variation as this is not uncommon in the Membracidæ. For this reason it would seem that taxonomic characters based on the shape, size and number of cells should not be attached with the greatest importance unless it can be clearly proven that these irregularities do not occur in the forms in question.

It may be mentioned in passing, that *Thelia bimaculata* shows also a great variation in the length of the pronotal horn. An attempt has been made to compare this variation with that of the wing but the results were negative, and the variation of the two structures seems to be entirely independent.

THE HIND WING

As has been stated (p. 81) the hind wing in the Membracidæ has more nearly kept pace with the fore wing in specialization than is usually the case in Hemiptera. An interpretation, therefore, of the fore wing leaves little to be determined so far as homologies are concerned and in fact the venation, after the tracheation has been worked out, is almost self-evident. In the hind wing the reduction has gone further than in the fore wing as is shown in the nymphal tracheation (Fig. 25). The tracheæ for costa and subcosta have disappeared. The wing, however, shows a thickening or ridge along the cephalic margin which is probably due to subcosta or perhaps in some cases to costa-plus-subcosta, although the preceding tracheæ are not distinguishable and the vein itself not prominent. Radius behaves much as in the fore wing. The trachea is apparently two-branched but high magnification shows that R_1 is present, running close to R_{2+3} (Fig. 26). Occasionally also, R_1 upon reaching the margin of the wing turns backward to meet the costal thickening so that in some cases the point at which costa-plus-subcosta unites with R_{2+3} represents what remains of R_1 (Fig. 27). The most important point of difference between the two wings is found in the cross vein r-m connecting R_{4+5} with M_{1+2}. This difference has been noted by Redtenbacher in his explanation of the hind wing of *Centrotus cornutus*[35] the only Membracid which he figures and which happens to show this character. In the fore wing these longitudinal veins (R_{4+5} and M_{1+2}) usually anastomose. In the hind wing

35. Redtenbacher, Josef. Vergleichende Studien uber das Flugelgeader der Insecten, Ann. k. k. Naturh. Hofmus. I, 1886, p. 187.

they are often some distance apart and connected by a strong cross-vein.[36] The explanation to the disappearance of costa and subcosta which causes this condition — which is of course the more generalized one — is probably that the median part of the wing, having an advantageous blood supply, has developed to such an extent as to crowd the cephalic region, causing radius to move over into that part of the wing usually occupied by costa and subcosta, and forcing these tracheæ out of existence.

Media is typical (Fig. 28), branching in about the center of the wing into M_{1+2} and M_{3+4} which continue their respective courses toward the tip, there to turn along the marginal line as in the fore wing.

Cubitus likewise presents the same condition that it does in the fore wing (Fig. 29). At times the tracheæ representing Cu_1 and Cu_2 respectively may be traced side by side for some distance back into the wing, but in no case do they separate.

First anal differs from the front wing in being stronger and not paralleling the suture. The wing membrane at this point in the hind wing is smooth and firm.

Second and third anals are usually coalesced to form one vein in the adult hind wing, although the individual tracheæ are to be seen in the nymphal structure. Occasionally these two veins separate to form the cell 2nd A as in *Ceresa bubalus*.

This is the normal venation. Some slight modifications can be found in a few genera. In *Smilia*, *Cyrtolobus*, *Xantholobus*, *Ophiderma*, and others, the characteristic cross-vein between R_{4+5} and M_{1+2} is lacking, these two veins anastomosing as in the front wing. In other respects the hind wings vary far less among the genera and species than in the fore wing, even in minor details. In many cases they are identical and it has been hard to find forms with differences marked enough to be worth figuring. It will be remarked in the figures that in shape and general appearance the agreement is quite noticeable.

36. See figures of *Carynota mera*, *Thelia bimaculata*, *Glossonotus crataegi*, *Telemona ampelopsidis*, *Archasia belfragei*, and *Heliria scalaria*.

BIBLIOGRAPHY.

The paper which has been the principal basis for this study and which has been a source of constant inspiration throughout the work, is Comstock-Needham's "Wings of Insects," published in the American Naturalist, Vols. XXXII and XXXIII, 1898 and 1899. Other publications and texts used are the following:

COMSTOCK. Manual for the Study of Insects.

STAL. Hemiptera Africana, Vol. IV.

GODING. Bibliographical and Synonymical Catalogue of the Described Membracidae of North America, Bulletin Illinois State Laboratory Natural History, Vol. 3, Art. XIV.

VANDUZEE. Studies in North American Membracidae, Bulletin Buffalo Society Natural Science, 1908, Vol. IX.

FOWLER. Biologia Centrali Americana, Insecta: Rhynchota, Homoptera Part II. Cambridge Natural History, Vol. VI, Insects, Part II.

MACGILLIVRAY. Wings of Tenthredinoidea, Proceedings U. S. Natural Museum, 1906, Vol. XXIX.

PATCH, MISS EDITH M. Homologies of the Wing Veins of the Aphididae, Psyllidae, Aleurodidae and Coccidae, Annals of the Entomological Society of America, 1909, Vol. II.

WOODWORTH. The Wing Veins of Insects, University of California Publications, Agricultural Experiment Station Technical Bulletin, Entomology, Vol. I,1906.

REDTENBACHER. Vergleichende Studien uber das Flugelgeader der Insecten, Ann. k. k. Naturh. I, 1886.

HODGKISS. The Apple and Pear Membracids, Geneva Agricultural Station Technical Bulletin No. 17, 1910.

FAIRMAIRE. Revue de la tribu des Membracides, Ann. de la Soc. Ent. de France, 1846, Ser. II, Tome IV.

SCHMIDT. Beitrag zur Kenntnis der Membraciden. Stett. ent. Ztg., 1906, Vol. 67.

FIGURES.

The figures of nymphal wings, and the diagrams used, are arbitrarily arranged in the order in which reference is made to them in the text, without respect to relationship of species.

The figures of adult wings are arranged according to subfamilies to facilitate reference. The order of subfamilies is based on Van Duzee's "Studies in North American Membracidae."

The following is the explanation of the figures in order:

Nymphal wings and diagrams.

Fig. 1. Fore and hind wings of Thelia bimaculata.
Fig. 2. Fore wing nymph—Thelia bimaculata.
Fig. 3. Fore wing nymph—Thelia bimaculata, showing costa.
Fig. 4. Fore wing nymph—Telemona ampelopsidis, showing costa.
Fig. 5. Fore wing nymph—Ceresa borealis, showing costa.
Fig. 6. Fore wing nymph—Vanduzea arquata, showing costa.
Fig. 7. Fore wing nymph—Vanduzea arquata, showing base of costa.
Fig. 8. Diagram showing typical radius.
Fig. 9. Fore wing nymph—Vanduzea arquata, showing R_1.
Fig. 10. Highly magnified portion of fore wing nymph of Vanduzea arquata, showing region of R_1.
Fig. 11. Highly magnified portion of fore wing nymph of Telemona ampelopsidis, showing region of R_1.
Fig. 12. Fore wing nymph—Enchenopa binotata, showing R_1.
Fig. 13. Fore wing nymph—Ceresa diceros, showing media and the coalescence of R_{4+5} with M_{1+2}.

Fig. 14. Base of fore wing nymph—Ceresa diceros, showing origin of media.
Fig. 15. Base of fore wing nymph—Thelia bimaculata.
Fig. 16. Fore wing nymph—Ceresa bubalus, showing anals.
Fig. 17. Fore wing nymph—Ceresa diceros, showing cubitus.
Fig. 18. Fore wing nymph—Thelia bimaculata, showing cross-vein.
Fig. 19. Fore wing nymph—Telemona ampelopsidis, showing anals.
Fig. 20. Fore wing nymph—Vanduzea arquata, showing 2nd and 3rd anals.
Fig. 21. Base of fore wing nymph—Thelia bimaculata, showing basal tracheation.
Fig. 22. Fore wing nymph—Ceresa bubalus, showing branches of longitudinal veins.
Fig. 23. Diagram of tracheation in tip of fore wing, showing formation of marginal vein.
Fig. 24. Diagram of variations in wing of Thelia bimaculata.
Fig. 25. Hind wing nymph—Thelia bimaculata.
Fig. 26. Highly magnified portion of hind wing nymph of Thelia bimaculata showing region of R_1.
Fig. 27. Diagram showing position of the remains of R_1 in hind wing.
Fig. 28. Hind wing nymph—Vanduzea arquata, showing media.
Fig. 29. Hind wing nymph—Ceresa diceros, showing cubitus.

Adult fore wings.

Fig. 30. Ceresa bubalus.
Fig. 31. Stictocephala lutea.
Fig. 32. Acutalis tartarea.
Fig. 33. Micrutalis calva.
Fig. 34. Micrutalis dorsalis.
Fig. 35. Carynota mera.
Fig. 36. Thelia bimaculata.
Fig. 37. Glossonotus crataegi.
Fig. 38. Telemona ampelopsidis.
Fig. 39. Telemonanthe pulchella.
Fig. 40. Archasia belfragei.
Fig. 41. Heliria scalari.
Fig. 42. Smilia camelus.
Fig. 43. Crytolobus vau.
Fig. 44. Atyma castaneae.
Fig. 45. Xanthlobus trilineatus.
Fig. 46. Ophiderma pubescens.
Fig. 47. Vanduzea arquata.
Fig. 48. Entylia bactriana.
Fig. 49. Publilia concava.
Fig. 50. Stictopelta marmorata.
Fig. 51. Platycotis sagittata.
Fig. 52. Campylenchia curvata.
Fig. 53. Enchenopa binotata.
Fig. 54. Tylopelta gibberata.
Fig. 55. Phylia ferruginosa.
Fig. 56. Centruchoides perdita.
Fig. 57. Platycentrus acuticornis.

Adult hind wings.

Fig. 58. Ceresa bubalus.
Fig. 59. Carynota mera.
Fig. 60. Thelia bimaculata.
Fig. 61. Glossonotus crataegi.
Fig. 62. Telemona ampelopsidis.
Fig. 63. Archasia belfragei.
Fig. 64. Heliria scalari.
Fig. 65. Smilia camelus.
Fig. 66. Cyrtolobus vau.
Fig. 67. Xantholobus trilineatus.
Fig. 68. Ophiderma pubescens.
Fig. 69. Vanduzea arquata.
Fig. 70. Stictopelta marmorata.
Fig. 71. Platycotis sagittata.
Fig. 72. Campylenchia curvata.
Fig. 73. Enchenopa binotata.
Fig. 74. Centruchoides perdita.